



Spatial and temporal fluctuations of the abundance of Neotropical cave-dwelling moth *Hypena* sp. (Noctuidae, Lepidoptera) influenced by temperature and humidity

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Abstract

The present study evaluated the seasonal variation of a population of *Hypena* sp. in the Gruta Taboa (Sete Lagoas, Minas Gerais, Brazil), in relation to changes in temperature and humidity during the dry (July 1999 and July 2000) and rainy (January 2000 and January 2001) seasons. The *Hypena* sp. population responded to external seasonality, being distributed closer to the cave entrance during the rainy season, in which temperature and humidity fluctuated around 21 °C and 85%, respectively. During the dry season abundance was higher in sections farther from the entrance (deeper sections) (19.2 °C temperature and 80% humidity). The results showed that this species is influenced by external environmental factors, even in a tropical region where the external climate fluctuations are lower compared to temperate regions.

Keywords

Noctuidae, Hypena, cave, seasonal variations, temperature, humidity, Neotropical

Introduction

Caves, in general, show little variation of environmental parameters such as temperature and humidity compared to the external environment. Thus, they are often considered more stable than the surrounding external environments (Poulson and White 1969, Howarth 1980, 1993).

According to Michell (1969), tropical caves are climatically more stable compared to temperate caves. However, the environmental conditions are not homogeneous throughout the cave, being composed by a series of microclimates which vary according to the cave area (Romero 2009). Characteristics like dimensions, width and number of cave entrances interfere on environmental parameters (Ferreira 2004).

Among the environmental parameters that influence the cave fauna is temperature, which is held as one of the main determinants of metabolic activities (Gillooly et al. 2001, 2002) and life history of organisms (Willott and Hassall 1998, Hodkinson et al. 1999). Parameters such as humidity and rainfall can also affect the ecology of several species (Rodrigues 2004).

In tropical regions, the seasonal fluctuations in the abundance and richness of insects are notorious and arise from the variation of temperature, humidity and rainfall (Wolda 1978). Such seasonal changes require specific strategies of the organisms that allow them to live under this variable conditions. Insects utilize many adaptations to avoid desiccation, including reduction of surface area and deposition of waxes and fat in the epicuticle, besides seeking for more stable environments or microhabitats with high humidity (Villani et al. 1999).

Many studies showed the effects of external climatic fluctuations on populations or subterranean communities in the temperate region (Bourne 1976, Bourne and Cherix 1978, Carchini et al. 1994, Novak et al. 2004, Tobin et al. 2013). These effects on population dynamics are farther expected in geographical regions where external climatic fluctuations are more intense (Michell 1969). However, modifications on cave population dynamics due to fluctuations of the external environmental parameters have been neglected in tropical regions, perhaps due to the false impression that both small temperature and humidity fluctuations (typical of tropical regions) have little or no effect on the subterranean fauna.

In this context, the present study aimed to determine seasonal variations in the spatial distribution and abundance of the population of the trogloxene moth *Hypena* sp. (Noctuidae, Lepidoptera) in a limestone cave in Southeastern Brazil.

Methodology

Study area

The study was conducted in a limestone cave with approximately 1000 meters of linear extension, called Taboa cave (19°28'30.0"S, 44°19'41.7"W – DMS (degrees, minutes,

seconds), located in the municipality of Sete Lagoas, Minas Gerais, Brazil. This cave is located in the Cerrado biome (Brazilian Savannah), however, the area surrounding the cave is quite altered, and much of the original vegetation has been removed for the establishment of pastures (Figure 1A). The climate classification is Cwa (Climate Warm or Humid Subtropical Climate), savanna climate with dry winter and humid summer with rain (Álvares et al. 2013). The average annual temperature in the municipality where the cave is located is 22.1 °C and the relative humidity varies around 70.5%. The average annual rainfall is 1,340 mm, with December as the rainiest month and August, the driest (Sans 1986).

Taboa cave comprises a vadose system and its main conduit is crossed (half of its extension) by a subterranean stream that enters the cave in its deepest part. The distal part of the cave is rather moist, and food resources include plant debris brought in by the water and especially bat guano. There is a small aperture (45×60 cm) in this distal part, which can not be used by humans due to the siltation which have strongly reduced the natural entrance. However, it can be used as an entrance for many invertebrates, although only few specimens of *Hypena* sp. (less than 10) were found in this area.

The area near the main entrance (which is also small -1.5 m high and 2 m wide) is quite dry throughout the year (Figure 1). Most of the *Hypena* sp. population lives near the main entrance (Figure 1) and the present study focused on this area.

Methods

The study was conducted within the first 120 m from the cave entrance. This part included the area where individuals of Hypena sp. were regularly found throughout the study. After the first 105 meters from the main entrance, specimens were eventually observed. These individuals observed after 105 meter from the main entrance were not considered in this study, since they were probably under the influence of the second opening, more than 650 meters distant from the main entrance of the cave. The first part of the cave was divided into five-meters sectors from the entrance to evaluate the temporal and spatial variations of Hypena sp. correlated to the seasonal variation of both temperature and humidity. Sampling was performed in the peaks of the dry periods (July 1999 and July 2000) and the peaks of the rainy periods (January 2000 and January 2001). The temperature and humidity measurements were taken in each sector once, every sampling period, by a digital thermohygrometer (Hygrotherm Oregon Scientific). The device was positioned on the cave floor and during the measurements the researcher stayed far from the device to prevent eventual influences on the cave atmosphere. Hypena sp. specimens were recorded in each sector and their distribution along the conduit was plotted on a cave sketch.

The surface temperatures and precipitation were obtained by consulting data from the National Institute of Meteorology (INMET), Sete Lagoas station, 16 km from the cave.



Figure 1. A Photograph indicating the cave entrance and the surrounding region, whose native forest was turned into pasture **B** Conduit located in the area near the entrance **C** Individuals of *Hypena* sp. resting on the cave wall.

Data analysis

The analysis of variance (ANOVA) was performed by using the R software in order to determine whether there were differences in abundance between sampling periods.

Since the data corresponds to a set of points that indicate the spatial location of each sampled individual inside the cave, we used Spatial Point Pattern Analysis (Diggle 2013, Bailey and Gatrell 1995, Gatrell et al. 1996). This analysis allowed to investigate the spatial relationships between individual occurrence points for each monitoring to identify spatial distribution patterns. The first step of this spatial analysis is to make a dot map. This enables an initial visualization of both the shape of the study area and the possible spatial pattern of the analyzed data (Bailey and Gatrell 1995). The spatial distribution patterns may be independent (completely random), regular or clustered. The next step is to evaluate the intensity of the point pattern. It corresponds to the average density of points, i.e., the expected number of points per unit area (Baddeley 2010). This evaluation allows describing how the expected value and mean vary across the space. Again, it is possible to identify by observing the intensity maps the existence of a possible spatial pattern and also if there are sectors in which individuals tend to cluster. The estimation of intensity values were made using an Isotropic Gaussian Kernel (Baddeley 2010, Gatrell et al. 1996). Subsequently, estimations of the K function together with simulation envelopes by the Monte Carlo method with 5,000 simulations (Baddeley 2010, Gatrell et al. 1996) were conducted to identify statistically the spatial patterns. According to Ripley (1981) the significance level of 5,000 simulations is about 0.0004. All analyses were performed in R software, Spatstat package (Baddeley and Turner 2005).

Results

Temporal variations of environmental parameters

The measured temperature in the studied cave stretch ranged from 18.6 °C to 23.1 °C. In the same period, the measured air relative humidity ranged from 50% to 96%.

During the dry periods the environmental parameters (humidity, precipitation and temperature) at the surface were relatively similar in the two sampling years. July 1999 showed no precipitation, the temperature fluctuated from 13 °C to 27 °C and the air relative air humidity was 60% (INMET 2008). July 2000 presented temperature varying from 12 °C to 26 °C and air relative humidity was 59.7% and there were 8.9 mm of precipitation (INMET 2008).

In January 2000 the temperature oscillated between 19.4 °C and 29.2 °C, with 74% air relative humidity and 387 mm of rainfall. In 2001, the same month had temperature, air relative humidity and precipitation of 18.8 °C–30.1 °C, 68.3% and 105.5 mm, respectively (INMET 2008).

The highest variation of temperature and humidity in the cave was observed near the entrance in both sampling periods (dry and rainy). As the distance from the entrance increased, there was an increase in humidity and a decrease in temperature until approximately halfway into the sampling area (70 m). However, in the final part of the study area the temperature tended to stabilize, a pattern that remained similar during the study (Figure 2A).

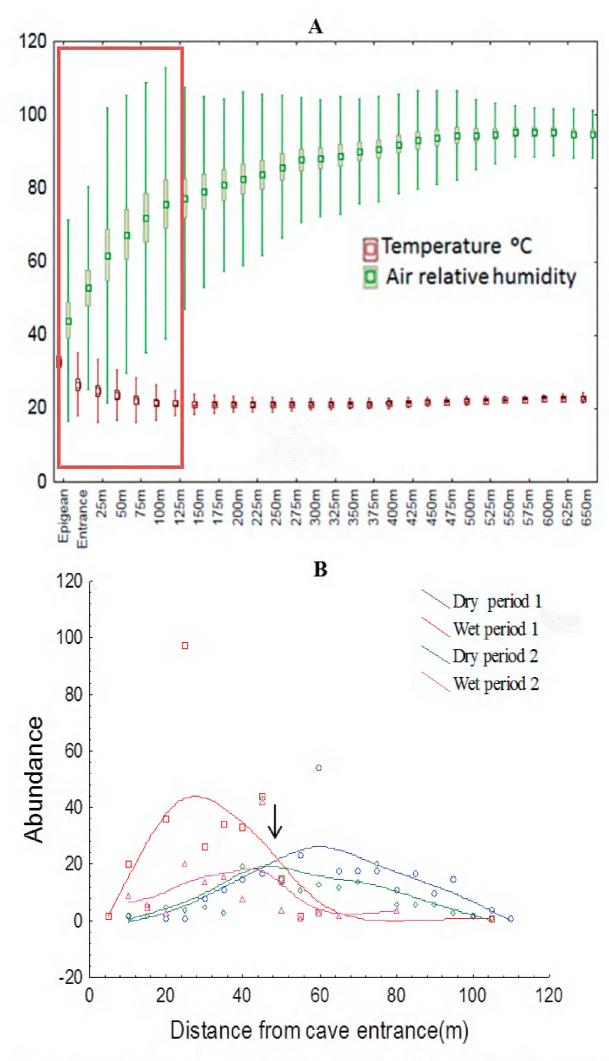


Figure 2. A Variation in temperature and humidity along the Taboa cave, showing a tendency to stabilize in the deeper parts of the cave. The table shows the section in which the *Hypena* sp specimens were collected (**B**) Change in abundance over the transects, the arrow indicates the spatial extent where the effects of the surface seasonality promote decrease and expansion in the population distribution.

Both temperature and humidity in the cave ranged in July 1999 (dry period), from 22.7 °C to 18.7 °C and 84–50%, respectively. In the following year (July 2000) the temperature and humidity ranged from 20.6 °C to 18.6 °C and 67 to 92%, respectively. The rainy season of 2000 (January) presented temperatures ranging from 23.7 °C to 20.5 °C and relative humidity from 71 to 91%. In the following year, the temperature and humidity ranged from 25 °C to 20.3 °C and 66–96%, respectively.

Temporal variations in the abundance of *Hypena* sp.

In the first visit to the cave (during the dry season – July, 1999) we observed 260 individuals of *Hypena* sp. while in the second visit (rainy season – January, 2000) we found 318 individuals. In the third visit, conducted in July, 2000 (dry season), we observed 192 individuals, and in the last visit (January, 2001 – rainy season) we observed 132 individuals. Accordingly, a total of 452 individuals of *Hypena* sp. were observed in the dry seasons and 450 during the rainy seasons. There were no significant differences in the number of individuals between the dry and rainy seasons (F = 0.522, df = 54, P = 0.6645). *Hypena* sp. individuals occurred in a temperature range between 18.6 °C and 25 °C and air relative humidity between 50 and 96%. Out of these intervals, no individuals were observed.

During the dry periods individuals were more abundant in the cave part where the temperature and humidity were around 19.2 °C and 80%, respectively, showing a preference for the areas farther inside the cave in this period. However, during the rainy seasons the organisms preferentially occupied areas closer to the entrance, where the temperature and humidity fluctuated around 21 °C and 85%, respectively.

During the rainy seasons, peaks of higher abundance were observed around 20 to 40 meters from the cave entrance. The peaks of abundance in the dry periods occurred slightly deeper inside the cave, around 50 to 70 meters from the cave entrance (Figure 2B).

Spatial analysis

Figure 3 summarizes the results obtained from the Spatial Point Pattern Analysis of the second visit to the cave (January 2000). In the dot map (Figure 3A) is the shape of the study area to see the distribution of the analyzed points. The observed individuals tend to concentrate in the innermost cave region, which possibly would feature a clustered pattern. This statement is confirmed by the K function estimations (Figure 3B), which allowed to identifying the spatial pattern of the data points. The theoretical K function refers to the expected values of this function assuming that points are completely random. The Monte Carlo method allowed to estimate the value upper and lower envelopes of the simulated K-functions defining the shaded region. This region corresponds to the completely random pattern. However, the empirical K function, which is estimated based on observed data, lies outside of this region indicating that the

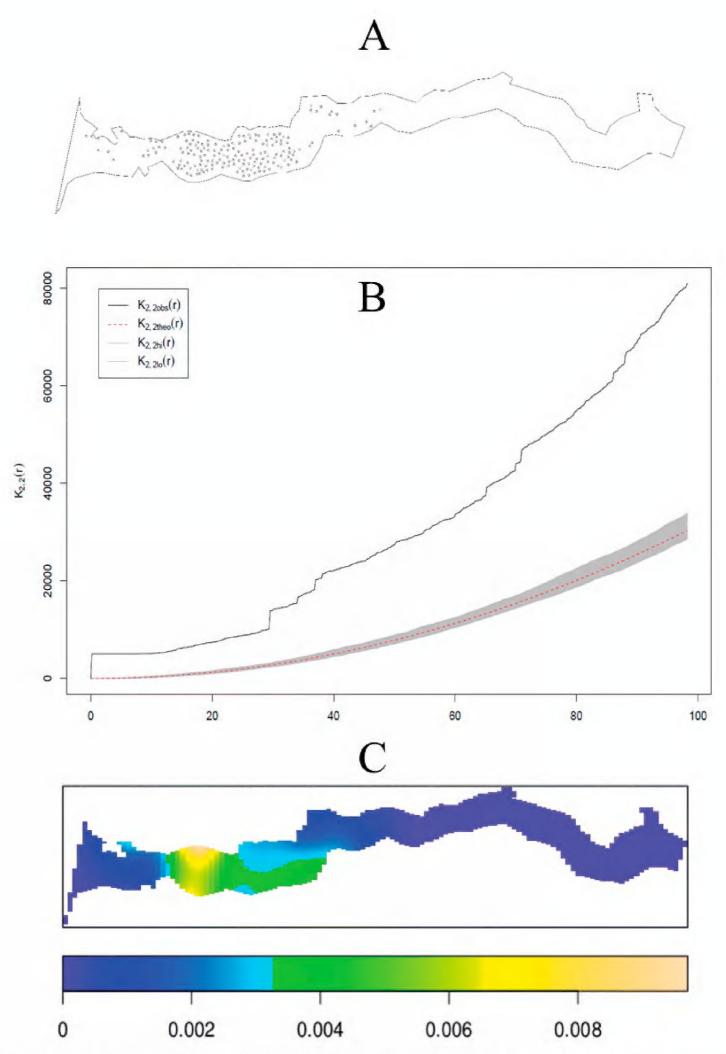


Figure 3. Spatial Point Pattern Analysis of the second monitoring (January 2000). **A** Dot map and (**B**), shows the estimations of the function K (r is the distance argument, Dashed line corresponds to the theoretical value of this function is Complete Spatial Randomness and solid lineis the Observed value of the K function for the date pattern) **C** Map Kernel Estimates of intensity.

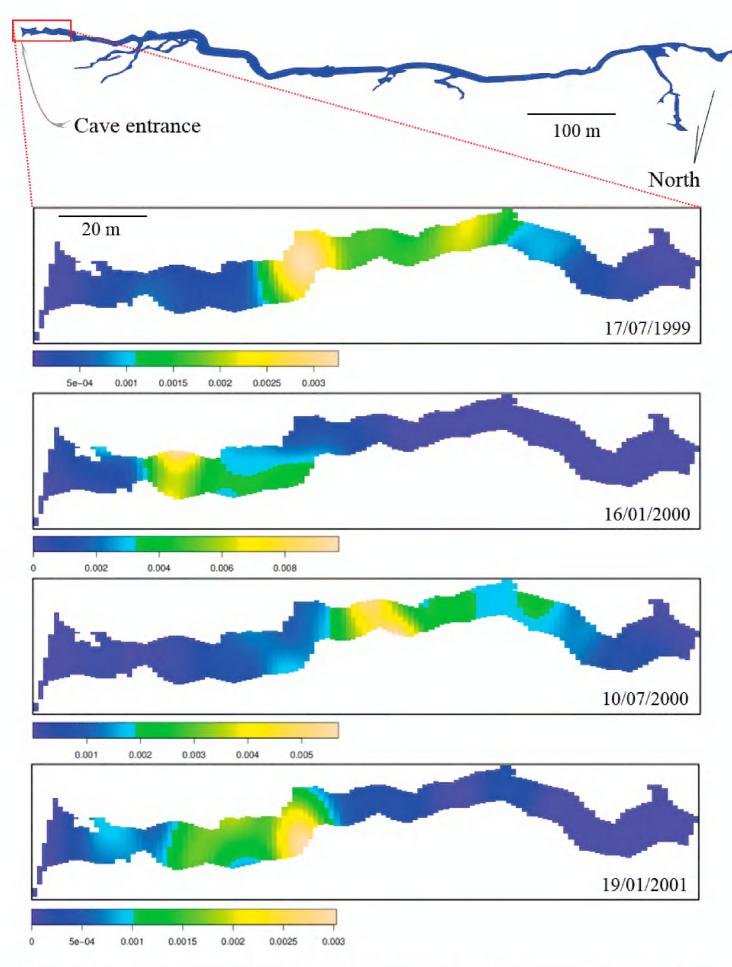


Figure 4. Spatial distribution maps of *Hypena* sp. demonstrating different densities between seasons. In the dry seasons (17/07/1999 and 10/07/2000) individuals are located in the deepest region of the cave, an opposite pattern during rainy seasons (16/01/2000 and 19/01/2001) when the population of individuals becomes denser in the region near the cave entrance. Blue colors indicate low densities while light yellow colors indicate high densities.

analyzed pattern is not random. Moreover, the values of this function are higher than those of the theoretical estimates, which characterize a clustered pattern. This pattern can also be seen in the intensity map (Figure 3C) in which regions with higher average density of points are observed. The clustered pattern observed in second sampling period (January 2000) has also been proven for all the other three sampling periods. The cluster spatial distribution has varied as follows: in July 1999 and July 2000, the sampled individuals concentrated in the innermost cave region, and in January 2000 and January 2001, clusters were observed in the region closer to the cave entrance (Figure 4).

Discussion

Both, the temperature and humidity varied between sampling periods and between the different cave sectors. However, the highest variations were observed near the entrance, where *Hypena* sp. preferentially occurred and presented the higher abundance. Although it is a trogloxene species and capable to support variable conditions the population has modified its spatial pattern of distribution, according to the variations of the external environment. The organisms tended to be distributed preferably in the regions farther from the entrance in the drier periods and in regions closer to the entrance in the wettest periods.

Caves have a tendency towards stability but cannot be characterized as closed systems (Bourgues et al. 2006), considering that during the winter the caves experience heat and humidity loss, countering the heat and humidity gain in the summer (Freitas 2010). In an environment that tends towards climate stability it is likely that even small variations can lead to alterations in species abundance or distribution (Tobin et al. 2013). Thus, the abiotic factors in a cave can also determine the local faunal distribution, especially considering insects, as observed in the present study.

The cave climate changes due to variations at the surface. During the cold winter, dry air enters the cave that in turn influences the desiccation of the organisms which are in direct contact with the air stream (Tuttle and Stevenson 2011). Evaporation is determined by the relative humidity and under high humidity the evaporation is low. However, if the relative humidity changes from 99.5% to 99%, the evaporation rate will double (Buecher 1999), what brings drastic physiological consequences to the fauna (Singh et al. 2009). Thus, it is plausible to assume that in order to avoid desiccation during the winter, specimens of *Hypena* sp. migrated to the inner regions of the cave, in search of higher humidity.

According to Bourne and Cherix (1978), *Triphosa dubitata* have a preference for environments where temperature and humidity are higher (>11 °C and 80%). The authors also noted that in response to seasonal changes of the air flow inside the cave, *T. dubitata* migrated in the winter to the inner regions to avoid low temperatures and desiccation.

Bourne (1976) in a study carried out in the La Scierie cave (France) showed that five species, among them two Lepidoptera (*Thiposa dubitata* and *T. sabaudiata*), mi-

grated during the autumn and winter to the inner regions of the cave. The previous studies reinforce the notoriety of the spatial variation of temporary cave fauna in temperate climates as a result of external changes. However, works in tropical regions showing a similar pattern are virtually non-existent.

According to Wolda (1978), in the tropics, the temperature variation is generally low and therefore the variables that best explain the seasonality of insects are humidity and precipitation. Although not carried out with a Lepidoptera, an interesting study performed by Carchini et al. (1994) showed seasonal variations in a cricket population of Dolichopoda geniculata in Valmarino Cave (Italy). It was observed that during summer the inner region of the cave presented a higher density of organisms, and during winter the population occupied the outmost area. This pattern was the opposite of the observed in the present study, but it should be noted that the cited work was performed under the Mediterranean climate (dry summer and rainy winter). Therefore, this fact suggests that humidity can exert great influence on the seasonality of these organisms, since the two studies previously mentioned (Bourne 1976, Carchini et al. 1994) showed that in the higher humidity period (rainy) the two populations of different species (from distinct groups) preferred the cave entrance area. McKillop (1993), studying caves in Canada, found moths (Triphosa haesitata) only in caves whose humidity was above 84%, leading to the belief that moisture is a limiting factor for the occurrence of this species.

Many species enter caves to avoid extreme temperatures (heat and cold) in order to establish themselves in an ideal or milder microclimate (Camp et al. 2007, Chelini et al. 2011). *Hypena* sp. showed a preference for a specific temperature and humidity range, and according to alterations of environmental parameters along the dry and rainy seasons, the population altered its distribution within the cave.

Although the tropical climate oscillates less than the temperate climate and supposedly there is less influence of these external climatic variations on the subterranean fauna, this study demonstrated that even small environmental fluctuations change the population dynamics of a species inhabiting caves. Therefore, we emphasize the importance of further studies, since most of the works in the tropics do not describe seasonal variation of environmental factors in caves, not even the response of organisms to these changes. Our results highlight the importance of monitoring population dynamics of cave invertebrates in relation to environmental conditions.

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References

- Álvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22(6): 711–728. doi: 10.1127/0941-2948/2013/0507
- Baddeley A (2010) Analysing spatial point patterns in R. CSIRO, 232 pp.
- Baddeley A, Turner R (2005) Spatstat: an R package for analyzing spatial point patterns. Journal of Statistical Software 12(6):1–42.
- Bailey C, Gatrell AC (1995) Interactive spatial data analysis. Longman Scientific & Technical, 413 pp. doi: 10.1080/02693799608902093
- Bourges F, Genthon P, Mangin A, D'Hulst D (2006) Microclimates of l'Aven d'Orgnac and other French limestone caves (Chauvet, Esparros, Marsoulas). International Journal of Climatology 26: 1651–1670. doi: 10.1002/joc.1327
- Bourne JD (1976) Notes preliminaire sur la distribuition spatiale de *Meta menardi*, *Triphosa dubitata*, *Triphosa sabaudiata*, *Nelima aurantiaca* et *Culex pipens* au seine d'un écosystème cavernicole (Grotte de La Sciere: Haut-Savoie). International Journal of Speleology 8: 253–267. doi: 10.5038/1827-806X.8.3.2
- Bourne JD, Cherix D (1978) Note sur l'écophase souterraine de Triphosa dubitata L. (Lep. Geometridae) et Scoliopteryx libatrix L. (Lep. Noctuidae). Bulletin de la Société Vaudoise des Sciences Naturelles 354(74): 147–156. doi: 10.5169/seals-277411
- Buecher B (1999) Microclimate study of kartchner caverns, Arizona. Journal of Cave and Karst Studies 61(2): 108–120.
- Camp CD, Jensen JB (2007) Use of twilight zones of caves by plethodontid salamanders. Copeia 2007(3):594–604. doi: 10.1643/0045-8511(2007)2007[594:UOTZOC]2.0.CO;2
- Carchini G, Rampini M, Sbordoni V (1994) Life cycle and population ecology of the cave cricket *Dolichopoda geniculata* (Costa) from Valmarino cave (Central Italy). International Journal of Speleology 23: 203–218. doi: 10.5038/1827-806X.23.3.6
- Chelini MC, Willemart RH, Gnaspini P (2011) Caves as a Winter Refuge by a Neotropical Harvestman (Arachnida, Opiliones). Journal Insect Behavior 24(5): 393–398 doi: 10.1007/s10905-011-9264-x
- Diggle PJ (2013) Statistical Analysis of Spatial and Spatio-Temporal Point Patterns. CRC Press, 267 pp.
- Ferreira RL (2004) A medida da complexidade ecológica e suas aplicações na conservação e manejo de ecossistemas subterrâneos. Tese (Doutorado em Ecologia, Conservação e Manejo da Vida Silvestre) Universidade Federal de Minas Gerais, Belo Horizonte, 158 pp.
- Freitas CR (2010) The role and importance of cave microclimate in the sustainable use and management of show caves. Acta Carsologica 39: 477–489.
- Gatrell AC, Diggle PJ, Rowlinsont BS (1996) Spatial point pattern analysis and its application in geographical epidemiology. Royal Geographical Society 21: 256–274. doi: 10.2307/622936
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of Size and Temperature on Metabolic Rate. Science 293: 2248–2251. doi: 10.1126/science.1061967

- Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of Size and Temperature on Developmental Time. Nature 417: 70–73. doi:10.1038/417070a
- Hodkinson ID, Bird J, Miles JE, Bales JS, Lennon JJ (1999) Climatic signals in the life histories of insects: the distribuition and abundance of heather psyllids (*Strophingia* spp.) in the UK. Funcional Ecology 13: 83–95. doi: 10.1046/j.1365-2435.1999.00011.x
- Howarth FG (1980) The Zoogeography of Specialized Cave Animals: A Bioclimatic Model. Evolution 34(2): 394–406. doi: 10.2307/2407402
- Howarth FG (1993) High-Stress Subterranean Habitats and Evolutionary Change in Cave-Inhabiting Arthropods. The American Naturalist 142: S65–S77. doi: 10.1086/285523
- INMET. Instituto Nacional de Meteorologia (2008) Banco de Dados da Estação Climatológica Principal, Embrapa Milho e Sorgo.
- Mckillop WB (1993) *Scoliopteryx libatrix* (Noctuidae) and *Triphosa haesitata* (Geometridae) in caves in Manitoba, Canada. Journal of the Lepidopterists' Society 47(2):106–113.
- Mitchell RW (1969) A Comparison of temperate and tropical cave communities. The southwestern Naturalist 14(1): 73–88. doi: 10.2307/3669249
- Novak T, Sambol J, Janžekovič F (2004) Faunal dynamics in the Železna Jama cave. Acta Carsologica 33(2): 249–267.
- Poulson TL, White WB (1969) The Cave. Environment. Science 165: 971–981. doi: 10.1126/science.165.3897.971
- Prous X, Ferreira RL, Martins RP (2004) Delimitation of epigean-hypogean ecotone zone in two limestone caves in southeastern Brazil. Austral Ecology 29: 374–382. doi: 10.1111/j.1442-9993.2004.01373.x
- Prous X, Ferreira RL, Jacobi C (2015) The entrance as a complex ecotone in a Neotropical cave. International Journal of Speleology 44: Article 5. http://scholarcommons.usf.edu/ijs/vol44/iss2/5
- Ripley BD (1981) Spatial statistics. John Wiley and Sons. doi: 10.1002/0471725218
- Rodrigues WC (2004) Fatores que influenciam no desenvolvimento dos insetos. Info Insetos 1(4): 1–4.
- Romero A (2009) Cave Biology: Life in Darkness. Cambridge University Press, 291 pp. doi: 10.1017/CBO9780511596841
- Sans LMA (1996) Estimativa do regime de umidade pelo método de Newhall, de um latossolo vermelho-escuro álico da região de Sete Lagoas, MG. Tese de Doutorado, Viçosa, UFV, 190 pp.
- Singh T, Bhat MM, Khan MA (2009) Insect Adaptations to Changing Environments -Temperature and Humidity. International Journal of Industrial Entomology 19(1): 155–164.
- Tobin BW, Hutchins BT, Schwartz BF (2013) Spatial and temporal changes in invertebrate assemblage structure from the entrance to deep-cave zone of a temperate marble cave. Journal of Speleology 42(3): 203–214. doi: 10.5038/1827-806X.42.3.4
- Tuttle MD, Stevenson DE (2011) Variation in the Cave Environment and its Biological Implications. BCI Bat Conservation and Management Workshop Arizona, 19–35.
- Villani MG, Allee LL, Díaz A, Robbin PS (1999) Adaptive strategies of edaphic arthropods. Annual Review of Entomology 44: 233–56. doi: 10.1146/annurev.ento.44.1.233

- Willott SJ, Hassall M (1998) Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. Functional Ecology 12: 232–241. doi: 10.1046/j.1365-2435.1998.00180.x
- Wolda H (1978) Seasonal fluctuations in rainfall, food, and abundance of tropical insects. Journal of Animal Ecology 47: 369–381. doi: 10.2307/3789